2002. The Journal of Arachnology 30:227–237

A PRELIMINARY MOLECULAR ANALYSIS OF PHYLOGENETIC RELATIONSHIPS OF AUSTRALASIAN WOLF SPIDER GENERA (ARANEAE, LYCOSIDAE)

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ABSTRACT. A data-set from the mitochondrial 12S rRNA gene subunit of 11 Australasian lycosid species (six New Zealand species and five Australian species) was generated. Three North American lycosid species, one European species and one New Zealand pisaurid (outgroup) were also sequenced. The sequence data for the 16 species were combined with the published sequences of 12 European lycosids, two Asian lycosids and one Asian pisaurid and were analyzed using parsimony and maximum likelihood analyses. The resulting phylogenetic trees reveal that Australasian species largely form clades distinct from Palearctic and Holarctic species providing further evidence against the placement of Australasian species in Northern Hemisphere genera. New Zealand wolf spiders appear to be related to a subset of Australian genera whereas the other Australian lycosid genera are related to Asian/Holarctic faunas. Gene sequences in the 12S region were useful when examining relationships between closely related genera, but were not as informative for deeper generic relationships.

Keywords: Lycosidae, New Zealand, Australia, lycosid genera, lycosid subfamilies

The monophyly of the Lycosidae is well supported (e.g. Dondale 1986; Griswold 1993), but at the subfamily level there is some disagreement (Dondale 1986; Zyuzin 1993; Dippenaar-Schoeman & Jocqué 1997) and lycosid genera, many of which are paraphyletic and polyphyletic, are in disarray. Although European lycosid generic placements are well established (e.g. Heimer & Nentwig 1991) and some Nearctic and African genera have been recently revised (e.g. Alderweireldt 1991, 1999; Dondale & Redner 1978, 1979, 1983a, 1983b; Russell-Smith 1982), a large number of the 2245 lycosid species (Platnick 2001) would seem to be misplaced. For example, a revision of the New Zealand lycosid fauna (Vink 2002) found that all but one described species were incorrectly placed in mostly Northern Hemisphere genera. Some of the confusion can be attributed to Roewer (1951, 1955, 1959, 1960) who described 65 lycosid genera of which only 31 are currently recognized (Platnick 2001); 12 of these are monotypic and many others contain only two species. Roewer's generic descriptions were short and based on highly variable, non-genitalic characters. Brignoli (1983) stated "it is apparent that most recent students of this group give little value to most of the genera described by Roewer in 1954 [1955] and 1960; still it is necessary to list them as no acceptable new 'system' has been yet proposed". However, Roewer cannot be held entirely responsible for the state of lycosid genera. Many of the generic problems are due to the morphological conservatism of the Lycosidae and the consequential lack of useful characters to define and separate genera.

In New Zealand and Australia, many early workers placed lycosid species into genera with which they were familiar in their native Europe (e.g. Koch 1877). In particular, *Lycosa* Latreille 1804, which is now considered to be a Mediterranean genus (Zyuzin & Logunov 2000), has been a convenient genus in which to place many new species or as a temporary home when genera need revising (e.g. McKay 1975). Many of the large, burrow-dwelling Australian species have been placed in *Lycosa* (e.g. *Lycosa godeffroyi* L. Koch 1865) but do not fit the genus as defined by Zyuzin & Logunov (2000). Rather, they have a genitalic morphology similar to *Geolycosa* Montgomery 1904 (sensu Dondale & Redner 1990).

Lycosids are among the numerically dominant arthropod predators found in open habi-

tats in Australasia (e.g. Forster 1975; Humphreys 1976; Churchill 1993; Sivasubramaniam et al. 1997; Hodge & Vink 2000; Framenau et al. 2002) and recent taxonomic work (Framenau 2002; Framenau & Vink 2001; Vink 2001, 2002) has addressed the generic placement of some Australasian species. New Zealand's fauna, comprising 27 species, has been revised (Vink 2002) with most species (20) in *Anoteropsis* L. Koch 1878. The Australasian genera *Allotrochosina* Roewer 1960 (two species), *Artoria* Thorell 1877 (17 species), *Notocosa* Vink 2002 (one species) and *Venatrix* Roewer 1960 (22 species) have been recently revised or reviewed (Framenau 2002; Framenau & Vink 2001; Vink 2001, 2002). There are also 12 Australian species that form "a natural grouping" and were placed in *Trochosa* C.L. Koch 1848 (McKay 1979) but none of these species fit the genus as defined by Dondale & Redner (1990). Australia has 141 described lycosid species and at least another 100 undescribed species (V.W. Framenau pers. comm.; CJV pers. obs.). The majority of Australian species appear to belong in *Artoria* and a *Geolycosa*-like genus (V.W. Framenau pers. comm.; CJV pers. obs.). Species in *Venatrix* and the *Geolycosa*-like genus have a pedipalpal configuration that places them in the Lycosinae Simon 1898 (Framenau & Vink 2001; CJV pers. obs.). Vink (2001) placed *Allotrochosina* in Venoniinae Lehtinen & Hippa 1979 (sensu Dondale 1986) and while the simple pedipalps of *Anoteropsis*, *Artoria*, *Notocosa* and the Australian species currently in *Trochosa* do not fit any of the current subfamily definitions (Framenau 2002; Vink 2002; CJV pers. obs.) they are perhaps closest to Venoniinae (sensu Dondale 1986). The phylogenetic position of Australasian genera within the Lycosidae is unknown.

Because lycosids are morphologically conservative it is unlikely that sufficient numbers of morphological characters could be found to infer phylogenetic relationships of Australasian genera to their counterparts in the rest of the world. Sequence data from a portion of the mitochondrial 12S rRNA gene of the small ribosomal subunit have yielded large data sets for phylogenetic analysis of spiders (e.g. Gillespie et al. 1994). Recently, 12S rRNA sequence data have been used to infer relationships among European lycosids (Zehethofer & Sturmbauer 1998; Vink & Mitchell 2002) and the relationship of Asian lycosids to other Lycosoidea (Fang et al. 2000). Zehethofer & Sturmbauer (1998) found that 12S rRNA was especially suitable for resolving relationships higher than the species level.

This preliminary study aimed to examine the relationship of exemplars of the major Australasian genera to exemplars of genera found elsewhere in the world using phylogenetic analyses of 12S rDNA sequence data.

METHODS

Generic placement of species was based on the latest catalog of Platnick (2001) and recent taxonomic revisions (Framenau 2002; Framenau & Vink 2001; Vink 2001, 2002). Species sequenced, sex, and collection details (locality, date and collectors) are shown in Table 1. All specimens are stored in 95% ethanol and refrigerated in the Ecology & Entomology Group, Lincoln University. Selected Australasian species represented the major species groups of Australia and New Zealand (Framenau 2002; Framenau & Vink 2001; Vink 2001, 2002; CJV pers. obs.). The North American species *Geolycosa rogersi* Wallace 1942, *Varacosa avara* (Keyserling 1877) and *Allocosa georgicola* (Walckenaer 1837) were sequenced and included in the analysis because of the similarity of their male pedipalp morphology to *Lycosa godeffroyi*. It should be noted that *Allocosa georgicola* does not fit the genus *Allocosa* Banks 1900 as defined by Dondale & Redner (1983b).

DNA extraction, amplification and sequencing.—Specimens were washed in sterile deionized, distilled water before DNA extraction. Total genomic DNA was extracted by homogenizing 1–2 legs from single individuals (Table 1) using a proteinase-K digestion and high salt precipitation method (White et al. 1990). Mitochondrial 12S regions were amplified using the following two primer combinations:

1) 12St-L (5′-GGTGGCATTTTATTTTATTAGAGG-3′) (Croom et al. 1991) plus 12Sbi-H (5′–AAGAGCGACGGGCGATGTGT-3′) (Simon et al. 1990), or
2) 12SR-N-14594 (5′-AAACTAGGATTAGATACCC-3′) plus 12SR-J-14199 (5′-TACTATGTTACGACTTAT-3′) (Kambhampati & Smith 1995) (Fig. 1).

Each 25 μl reaction consisted of 1× *Taq*

Table 1.—Specimens sequenced showing species, sex, collection localities, collectors and dates collected, primers used and GenBank accession numbers.

Species	Sex	Collection details	Primers used	GeneBank accession no.
Allocosa georgicola (Walckenaer 1837)	female	USA, near Oxford (34°13′N, 89°19′W), 12.x.1999, L. Schaffer	12SR-J + 12SR-N	AF380499
Alopecosa barbipes (Sundevall 1833)	male	England, Redgrave & Lopham Fen (52°23′N, 01°00′E), 6.x.1999, C.J. Vink & M.A. Hudson	12St-L + 12Sbi	AY028420
Allotrochosina schauinslandi (Simon 1899)	female	New Zealand, Prices Valley (43°48′S, 172°41′E), 12.vi.1999, C.J. Vink & J.W. Griffiths	12St-L + 12Sbi	AF380502
Anoteropsis adumbrata (Urquhart 1887)	female	New Zealand, Titan Rocks (45°32′S, 169°00′E), 9.xii.1998, G. Hall, B. Brown & E. Edwards	12St-L + 12Sbi	AF380491
Anoteropsis lacustris Vink 2002	male	New Zealand, Arthur's Pass (42°56′S, 171°34′E), 9.iv.1999, C.J. Vink & M.A. Hudson	12St-L + 12Sbi	AF380489
Anoteropsis senica (L. Koch 1887)	male	New Zealand, Franz Josef Glacier (43°25′S, 170°10′E), iv.1999, C.J. Vink & M.A. Hudson	12SR-J + 12SR-N	AF380490
Artoria flavimanus Simon 1909	male	Australia, Crowea (34°28′S, 116°10′E), 6.v.1999, C.J. Vink	12SR-J + 12SR-N	AF380492
Dolomedes minor L. Koch 1876	female	New Zealand, Lake Ellesmere (43°43′S, 172°30′E), 20.xi.1999, R.M. Emberson	12SR-J + 12SR-N	AF380503
Geolycosa rogersi Wallace 1942	female	USA, Avent Park 34°13′N, 89°18′W), 1.iv.2000, G. Stratton, P. Miller & B. Suter	12SR-J + 12SR-N	AF380498
Lycosa godeffroyi L. Koch 1865	female	Australia, Bellerive (42°52′S, 147°22′E), 11.v.1999, C.J. Vink & J. Cossum	12SR-J + 12SR-N	AF380497
Notocosa bellicosa (Goyen 1887)	male	New Zealand, Temuka (44°14′S, 171°17′E), iii.1999, M. Ross	12SR-J + 12SR-N	AF380493
Trochosa oraria (L. Koch 1876)	female	Australia, Lauderdale (42°55′S, 147°29′E), 11.v.1999, C.J. Vink & J. Cossum	12St-L + 12Sbi	AF380501
Varacosa avara (Keyserling 1877)	male	USA, Sardis Reservoir (34°15′N, 89°28′W), 14.ix.1999, G. Stratton & W. Calvert	12SR-J + 12SR-N	AF380500
Venatrix goyderi (Hickman 1944)	female	New Zealand, near Matarau (35°38′S, 174°11′E), 15.ii.1999, C.J. Vink	12St-L + 12Sbi	AF380496
Venatrix lapidosa (McKay 1974)	male	Australia, Avon River (37°48′S, 146°57′E), iii.1999, V.W. Framenau	12SR-J + 12SR-N	AF380495
Venatrix pictiventris (L. Koch 1877)	male	Australia, Queens Domain (42°52′S, 147°19′E), 9.v.1999, C.J. Vink	12St-L + 12Sbi	AF380494

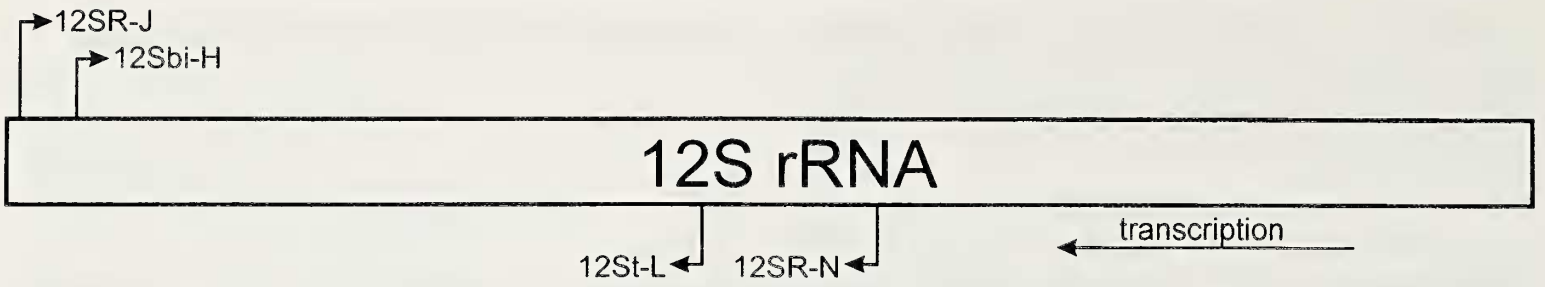


Figure 1.—Gene region coding for 12S rRNA showing areas sequenced by primers and direction of transcription.

buffer, 0.25 mM dNTPs, 2 mM $MgCl_2$, 0.4 μM of each primer, 1.25 units *Taq* DNA Polymerase (Roche) and 1μl of genomic DNA [which was diluted 1:20 in TE (10 mM Tris, 1 mM EDTA, pH 8.0) and used as a template for the amplification of double-stranded DNA (dsDNA)]. Amplification was performed in a GeneAmp® PCR System 2400 (Perkin–Elmer) thermocycler and the following temperature profile was used: 4 min. at 94 °C; 40 cycles of 20 s at 94 °C, 30 s at 50 °C, 40 s at 72 °C; 2 min. at 72 °C. Excess primers and salts were removed from the resulting dsDNA by precipitation with 100% isopropanol in the presence of 2.5M NH_4Ac, followed by a 70% ethanol wash. Purified PCR fragments were sequenced using ABI PRISM® BigDye™ termination mix version 1 (Perkin-Elmer) and separated on an ABI PRISM® 373 automatic sequencer. The sense and antisense strands were sequenced for all species except *Venatrix pictiventris* L. Koch 1877 and *Anoteropsis lacustris* Vink 2002, which were successful only one way. Sequence data were deposited in GenBank (Benson et al. 2000) (see Table 1 for accession numbers).

Data analysis.—Sequences were aligned to 15 previously published sequences (Zehethofer & Sturmbauer 1998; Fang et al. 2000) (Table 2) using Clustal W 1.7 (Thompson et al. 1994), then confirmed by eye. Insertion/deletion events were inferred where necessary based on the secondary structure of 12S rRNA proposed by Hickson et al. (1996). Although Hickson et al. (1996) used the 12S sequence of *Tetragnatha mandibulata* Walckenaer 1842 when constructing their template, helix 42 did not seem to be present in the lycosid or pisaurid sequences. In order to match the data obtained by Zehethofer & Sturmbauer (1998) sequence data that began five bases downstream from where the 12St-L primer annealed to seven bases upstream from where the 12Sbi-H primer annealed were included in

Table 2.—Other published sequences used in analyses showing species, reference and Genebank accession numbers.

Species	Reference	GenBank accession no.
Alopecosa accentuata (Latreille 1817)	Zehethofer & Sturmbauer (1998)	AJ008022
Alopecosa pulverulenta (Clerck 1757)	Zehethofer & Sturmbauer (1998)	AJ008025
Arctosa leopardus (Sundevall 1833)	Zehethofer & Sturmbauer (1998)	AJ008032
Dolomedes raptor Bösenberg & Strand 1906	Fang et al. (2000)	AF145031
Lycosa coelestis L. Koch 1878	Fang et al. (2000)	AF145030
Pardosa agrestis (Westring 1861)	Zehethofer & Sturmbauer (1998)	AJ008033
Pardosa hortensis (Thorell 1872)	Zehethofer & Sturmbauer (1998)	AJ008007
Pardosa palustris (Linnaeus 1758)	Zehethofer & Sturmbauer (1998)	AJ008011
Pardosa takahashii (Saito 1936)	Fang et al. (200)	AF145032
Pirata hygrophilus Thorell 1872	Zehethofer & Sturmbauer (1998)	AJ008015
Pirata knorri (Scopoli 1763)	Zehethofer & Sturmbauer (1998)	AJ008019
Trochosa terricola Thorell 1856	Zehethofer & Sturmbauer (1998)	AJ008017
Trochosa spinipalpis (F.O.P.-Cambridge 1895)	Zehethofer & Sturmbauer (1998)	AJ008016
Xerolycosa miniata (C.L. Koch 1834)	Zehethofer & Sturmbauer (1998)	AJ008021
Xerolycosa nemoralis (Westring 1861)	Zehethofer & Sturmbauer (1998)	AJ008020

the analyses. The analyses were conducted using PAUP* 4.0b4a (Swofford 2000).

Data were analyzed as unordered characters, first using parsimony and the heuristic search (1000 replicates) option in PAUP*. All characters were equally weighted, and zero length branches were collapsed to polytomies. Bootstrap values (Felsenstein 1985) were calculated from 1000 replicate parsimony analyses using the heuristic search option in PAUP*. Modeltest version 3.06 (Posada & Crandall 1998) was used to select the maximum likelihood parameters, GTR+Γ+I. The general time reversible model (Yang 1994) was used to estimate the maximum likelihood tree and branches were collapsed (creating polytomies) if the branch length was less than or equal to 1e–08. The maximum likelihood analysis included 20 taxa. Taxa were pruned if they were part of a well-supported node (bootstrap value >75%) in the parsimony tree leaving one representative of each taxon. Bootstrap values were calculated from 100 replicate likelihood analyses using the heuristic search option in PAUP*.

RESULTS

The primer combination 12St–L plus 12Sbi–H produced a single amplification product for seven species (see Table 1), but two or more bands were amplified for all other taxa. The primer pair 12SR–J–14199 plus 12SR–N–14594 was used to amplify product for sequencing for the taxa that did not produce a single amplification product using the 12St–L plus 12Sbi–H combination (see Table 1). The 12St–L primer site varied considerably in the nine taxa for which the primer pair 12SR–J–14199 plus 12SR–N–14594 was used, which may explain why the primer combination 12St–L plus 12Sbi–H did not work for all taxa. The primer 12St–L was designed as a *Tetragnatha*-specific primer (Croom et al. 1991) so it is not surprising that this site varies in lycosids. There was little variation evident in the 12Sbi-H site even though this primer was designed as specific to insects (Simon et al. 1990). The nucleotide composition was A + T-rich (44.2% A, 10.0% C, 9.8% G, 36.0% T), which is typical for arthropods (Simon et al. 1994).

Parsimony analysis yielded 2 equally parsimonious trees (Fig. 2), 482 steps long, with a consistency index, excluding uninformative characters, of 0.415 and retention index of 0.577. Of the 330 characters included in the analysis, 172 were variable with 113 of them parsimony informative. Maximum likelihood analysis resulted in six trees with scores of 2092.1969 (Fig. 3). The six trees had the same topology because the branches were collapsed (creating polytomies) if the branch length was less than or equal to 1e–08. The topology of the maximum likelihood trees (Fig. 3) and the parsimony trees (Fig. 2) differed mainly in the lower branches, which had less than 50% bootstrap support.

DISCUSSION

Molecular analysis confirms that most of the New Zealand or Australian lycosids included in the analysis do not belong in the Northern Hemisphere genera where they have been or are currently placed. This study confirms that *Trochosa oraria* L. Koch 1876 does not belong in the genus *Trochosa* (sensu Dondale & Redner 1990) and the two Holarctic exemplars of *Trochosa* are monophyletic, which is supported by high bootstrap values (Fig. 2). There is support for the monophyly of *Pardosa* C.L. Koch 1847 as the four exemplars form a monophyletic clade that is supported by a high bootstrap value (Fig. 3). Zehethofer & Sturmbauer (1998) also had strong support for the monophyly of the 14 exemplars of *Pardosa* that they included in their analysis. The three exemplars of *Alopecosa* Simon 1885 included in this study form a strongly supported monophyletic clade, as did the six exemplars included in the analysis of Zehethofer & Sturmbauer (1998). The exemplars of *Xerolycosa* Dahl 1908 and *Pirata* Sundevall 1833 both have good support for their monophyly. The molecular evidence suggests that *Allocosa georgicola* belongs in a *Geolycosa*-like genus, however, there is poor bootstrap support and no *Allocosa* species (sensu Dondale & Redner 1983b) were included in this analysis. *Lycosa coelestis* L. Koch 1878 does not fit the genus *Lycosa* as defined by Zyuzin & Logunov (2000) and comes out as sister to *Varacosa avara* in both analyses with reasonable bootstrap support. However, Dondale & Redner (1990) stated that *Varacosa* Chamberlin & Ivie 1942 is restricted to North America. Both trees (Figs. 2, 3) support the monophyly of the clade containing spiders with *Geolycosa*-like pedipalps

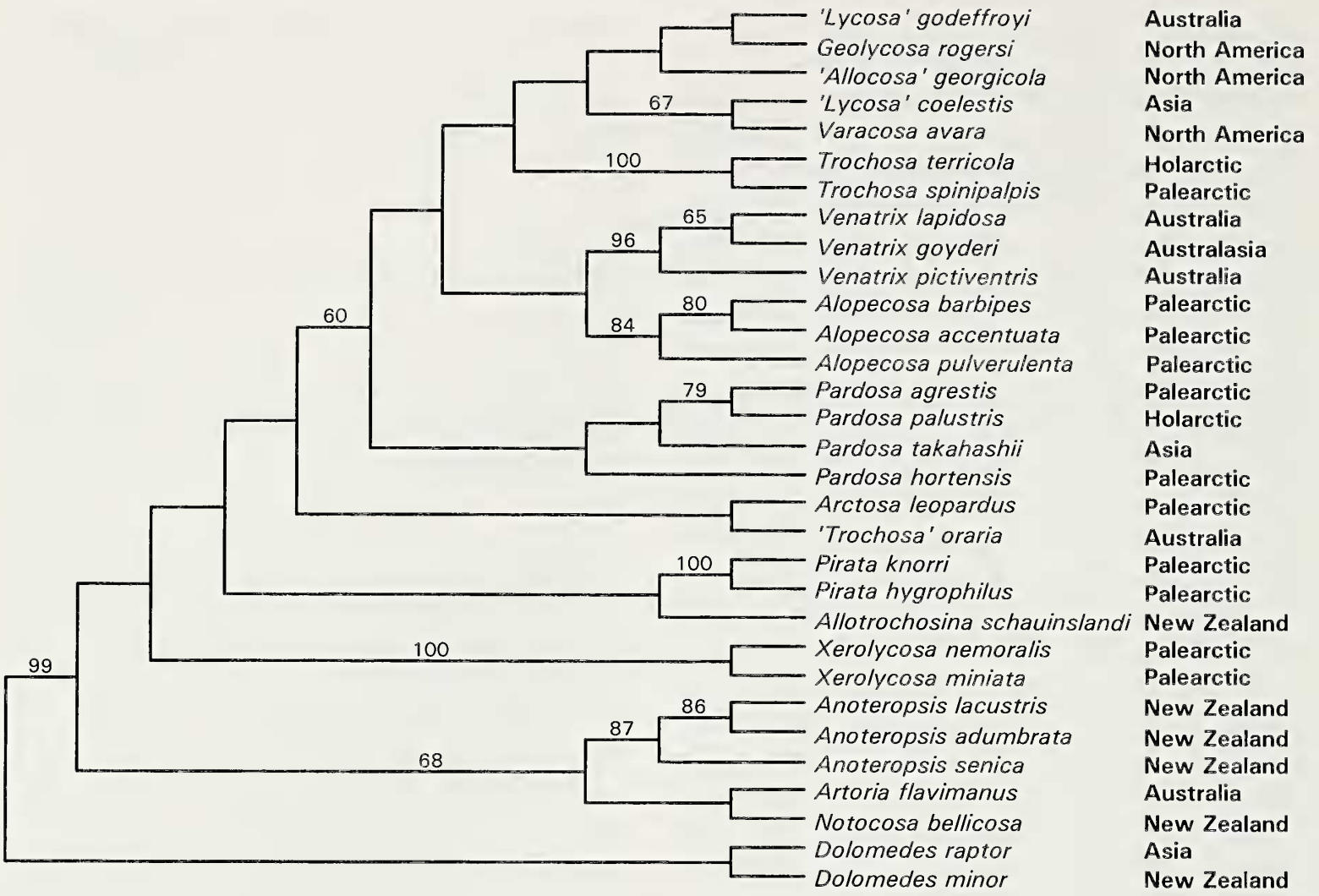


Figure 2.—One of two most parsimonious trees. The other tree differed by switching the positions of *Lycosa godeffroyi* and *Allocosa georgicola*. Bootstrap values above 50% are indicated above branches. Species distributions based on Platnick (2001) are shown on the right. Species that do not fit current generic definitions have the generic name in inverted commas.

(*L. godeffroyi*, *G. rogersi*, *A. georgicola*, *L. coelestis* and *V. avara*) but there is low (< 50%) bootstrap support for this clade. The Mediterranean genus *Lycosa* (sensu Zyuzin & Logunov 2000) is unlikely to be appropriate for *L. godeffroyi* but this cannot be inferred from our analyses because we did not sequence any Mediterranean *Lycosa* species. However, both analyses have *L. godeffroyi* coming out with *Geolycosa rogersi*, which is a true *Geolycosa*. The strongly supported, monophyletic clade of three *Venatrix* exemplars supports the monophyly of *Venatrix*. In both analyses (Figs. 2, 3) *Venatrix* was sister to *Alopecosa* and it has been noted that they share a similar pedipalpal structure (Framenau & Vink 2001). The clade containing the three *Anoteropsis* exemplars is monophyletic, which concurs with Vink (2002). *Anoteropsis* and *Notocosa* appear to be restricted to New Zealand (Vink 2002) and *Artoria* are most diverse in Australia but are also found in New Zealand, Papua New Guinea and the Philippines (Framenau 2002; Vink 2002). The monophyly of the clade containing exemplars from *Anoteropsis*, *Artoria* and *Notocosa* is supported in both analyses and all five species share a similar pedipalp configuration (Figs. 4–8) that includes a partially divided tegulum and similarities in the position and shape of the median apophysis (Vink 2002). The relationship of *Notocosa bellicosa* (Goyen 1887) to the other four species in the clade differs between the analyses. The parsimony analysis puts *N. bellicosa* as sister to *Artoria flavimanus* Simon 1909, whereas the bootstrap support (61%) within the parsimony trees and maximum likelihood analysis have *N. bellicosa* as sister to a clade containing the other four species. This clade does not fit current subfamily definitions and, once the genera are revised, may be placed in its own subfamily.

When *Trochosa oraria* is not included in *Trochosa*, the subfamilies Pardosinae Simon 1898 and Lycosinae Simon 1898 as defined by Dondale (1986) are supported, except for *Arctosa* C.L. Koch 1847, which falls outside the Lycosinae in this analysis. Dondale (1986)

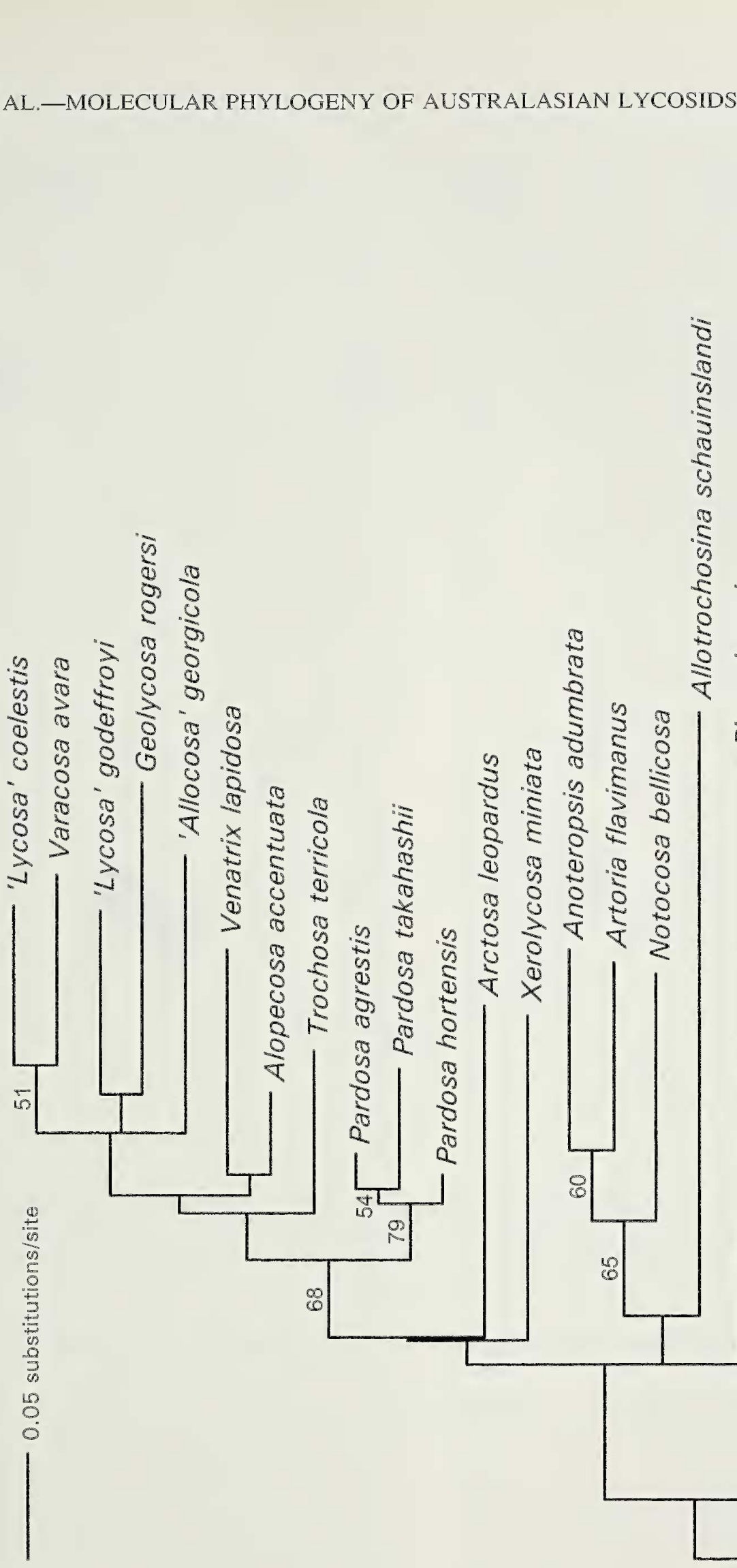
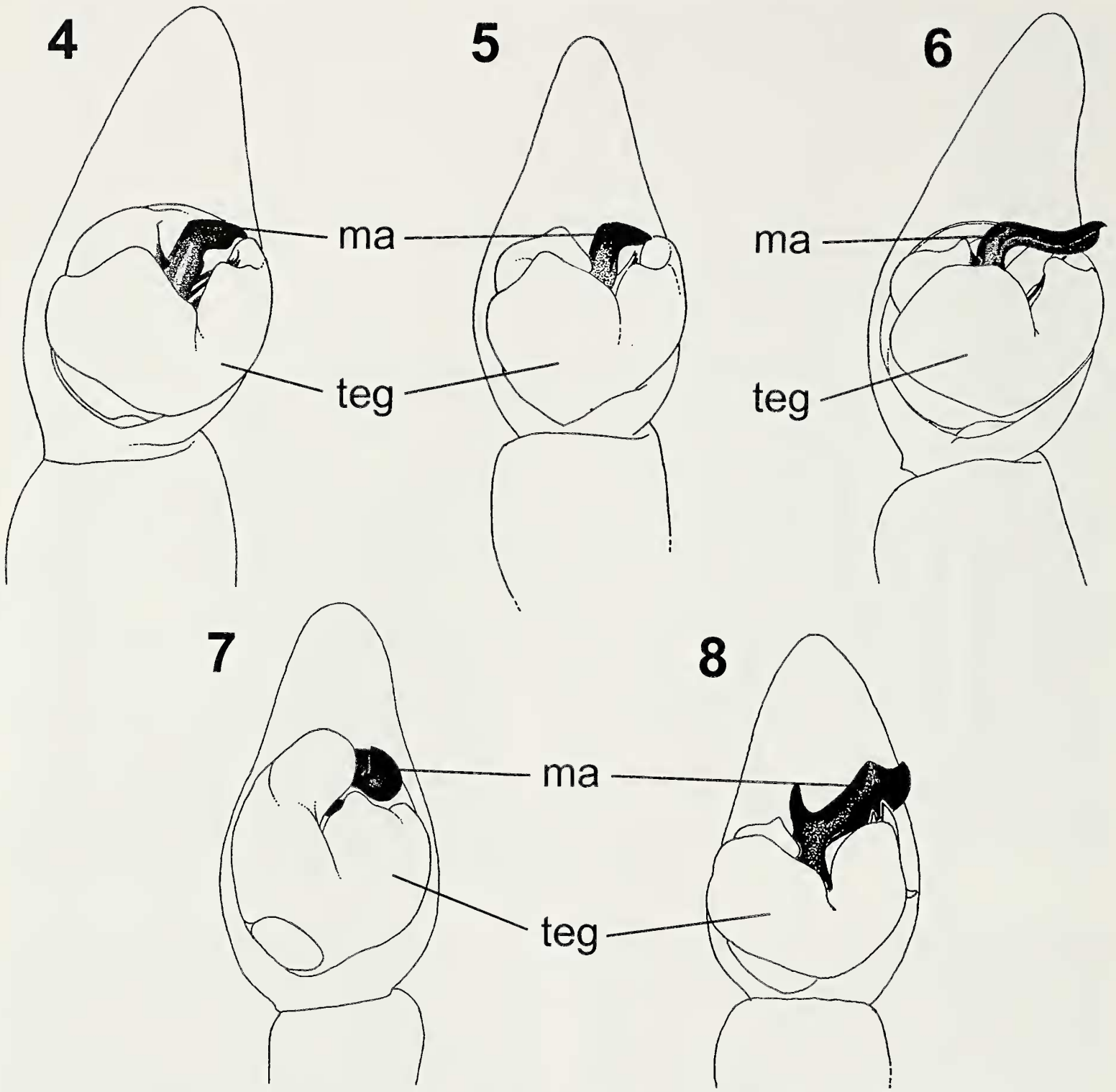


Figure 3.—Strict consensus of the six maximum likelihood trees. Bootstrap values above 50% are indicated above branches. Branch lengths are proportional to nucleotide substitutions. Species that do not fit current generic definitions have the generic name in inverted commas.



Figures 4–8.—Palps of (4) *Anoteropsis adumbrata*, (5) *Anoteropsis lacustris*, (6) *Anoteropsis senica*, (7) *Notocosa bellicosa* and (8) *Artoria flavimanus* showing partially divided tegulum (teg) and similarities in position and shape of median apophysis (ma).

suggested that the Lycosinae be divided into the "*Trochosa* group" and the "*Lycosa* group" but they are paraphyletic in our analyses. The placement of *Allotrochosina* in the subfamily Venoniinae (which also includes *Pirata* Sundevall 1833) by Vink (2001) is supported by the parsimony tree (Fig. 2) but not by the maximum likelihood tree (Fig. 3). It is worth noting that there is little bootstrap support for the lower branches of either tree. Further sequencing of several other genera may resolve these subfamily relationships.

While the pattern of distribution fits with a Gondwanan scenario a more detailed study of genetic divergence may reveal a better approximation of the time the faunas have been separated. Preliminary analyses presented here (Figs. 2, 3) imply that Australasia had an ancestral fauna and was subsequently invaded by lycosine species, possibly via Asia through northern Australia. When New Zealand split away from Australia about 80 million years ago (Stevens et al. 1988), it is likely it retained an ancestral lycosid fauna. Only two lycosine species (*Venatrix goyderi* (Hickman 1944) and *Geolycosa tongatabuensis* (Strand 1911)) are found in New Zealand and it is likely that they have subsequently ballooned across to

New Zealand; both species are widely distributed across Australia and the South Pacific respectively but, in New Zealand, they are limited to the warmer north of the North Island.

The phylogenies presented here are somewhat preliminary, as some genera found in Australia are not represented (e.g. *Anomalosa* Roewer 1960, *Venonia* Thorell 1894, *Zoica* Simon 1898). Further resolution of subfamily relationships could also be facilitated by the inclusion of exemplars from Allocosinae Dondale 1986, Sosippinae Dondale 1986, Tricassinae Alderweireldt & Jocqué 1993, and Wadicosinae Zyuzin, 1985. The inclusion of at least one exemplar from *Lycosa* (sensu Zyuzin & Logunov 2000) may help to confirm the relationship of that genus to other lycosine genera.

Results presented here suggest that 12S DNA sequence data are useful for inferring phylogenies of closely related genera. However, these data appear to be too conservative for adequate resolution at the species level (Vink & Mitchell 2002) and too fast for deeper relationships, inferred from bootstrap support of less than 50% shown for the lower branches of the parsimony tree (Fig. 2). Deeper relationships in the Lycosidae may be better resolved by the use of an even more slowly evolving gene region, such as 28S rDNA, which has been used to infer spider phylogeny at the family level (Hausdorf 1999).

In summary, we conclude that many current generic placements of Australasian species are incorrect; the New Zealand fauna is related to a subset of the Australian fauna and parts of the Australian fauna are related to the Asian/Holarctic fauna, suggesting a subsequent invasion. Current subfamilies were found to be largely monophyletic but further work is required to fully resolve subfamily relationships.

ACKNOWLEDGMENTS

We thank the following people for help with the collection of fresh specimens: Marie Hudson, Jeff Cossum (Tasmanian Museum & Art Gallery), Volker Framenau (University of Melbourne), Grace Hall (Landcare Research), Rowan Emberson (Lincoln University) and Philip Howe (South Canterbury Museum). Thanks to Gail Stratton (University of Mississippi) for collecting and sending fresh specimens from the US. We are indebted to Dianne Gleeson (Landcare Research) and Martyn Kennedy (University of Glasgow) for assisting with maximum likelihood analyses. Volker Framenau, Phil Sirvid and Eric Scott provided helpful comments on the manuscript. This research was made possible by funding from Landcare Research, the Miss E.L. Hellaby Indigenous Grasslands Research Trust and the Soil, Plant and Ecological Sciences Division, Lincoln University.

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Manuscript received 1 July 2001, revised 4 February 2002.